

Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods

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Received January 31, 1984¹

Accepted June 20, 1984

FEDERER, C. A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* **14**: 763–767.

Organic content of the forest floor decreases for several years after clear-cutting, and then slowly recovers. Thickness, bulk density, organic matter, and nitrogen content of forest floors were measured for 13 northern hardwood stands in the White Mountains of New Hampshire. Stands ranged from 1 to about 100 years in age. Forest-floor thickness varied significantly with stand age, but bulk density, organic fraction, and nitrogen fraction were independent of age. Total organic content of the forest floor agreed very well with data from Covington's (W. W. Covington 1981. *Ecology*, 62: 41–48) study of the same area. Both studies indicated that mature forest floors have about 80 Mg organic matter \cdot ha⁻¹ and 1.9 Mg nitrogen \cdot ha⁻¹. Within 10 or 15 years after cutting, the organic matter content of the floor decreases to 50 Mg \cdot ha⁻¹, and its nitrogen content to 1.1 Mg \cdot ha⁻¹. The question whether the decrease is rapid and the minimum broad and flat, or if the decrease is gradual and the minimum sharp, cannot be answered. The subsequent increase to levels reached in mature forest requires about 50 years. Some of the initial decrease in organic matter and nitrogen content of the forest floor may be caused by organic decomposition and nitrogen leaching, but mechanical and chemical mixing of floor into mineral soil, during and after the harvest operation, may also be important. The difference is vital with respect to maintenance of long-term productivity.

FEDERER, C. A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* **14**: 763–767.

La masse de matière organique de la couverture morte décroît durant plusieurs années après une coupe à blanc et, subséquemment, elle se reconstitue lentement. L'auteur a mesuré l'épaisseur, la densité apparente, le contenu en matière organique et en azote de la couverture morte de 13 peuplements de feuillus nordiques dans les White Mountains du New Hampshire. L'âge des peuplements se situait entre 1 et 100 ans. L'épaisseur de la couverture morte variait significativement avec l'âge du peuplement, mais la densité apparente et la proportion de matière organique et d'azote en étaient indépendantes. Les données de l'auteur sur le contenu total en matière organique de la couverture morte concordaient très bien avec celles d'une étude antérieure pour la même région (W. W. Covington 1981. *Ecology*, 62: 41–48). Les deux études indiquaient que les couvertures mortes renferment environ 80 Mg \cdot ha⁻¹ de matière organique et 1,9 Mg \cdot ha⁻¹ d'azote à maturité. Au cours des 10–15 années suivant la coupe, le contenu en matière organique de la couverture morte diminue jusqu'à 50 Mg \cdot ha⁻¹ et son contenu en azote, jusqu'à 1,1 Mg \cdot ha⁻¹. On ne peut dire, cependant, si la diminution est rapide et le minimum étendu et stable ou la diminution graduelle et le minimum aigu. L'augmentation subséquente aux niveaux atteints en forêt mature nécessite environ 50 ans. Une partie de la diminution initiale des contenus en matière organique et en azote de la couverture morte peut être causée par la décomposition organique et le lessivage de l'azote, mais le mélange mécanique et chimique de la couverture morte au sol minéral, durant et après les opérations de récolte, peut aussi jouer un rôle important. La différence est vitale pour le maintien de la productivité à long terme.

[Traduit par le journal]

Introduction

Modern forest management frequently includes clear-cutting, short rotations, and high utilization. Nutrient removal in harvested products and nutrient loss by leaching under such management has caused concern about maintenance of long-term nutrient status and forest productivity (Hornbeck 1977; Kimmins 1977).

The forest floor is a major source of nutrients in many forest types. Where the forest floor is a mor, root density and microbial activity are much greater in the floor than in the mineral soil. The status of nitrogen, which is the most frequently limiting nutrient in many forests (Anonymous 1973), is closely tied to the status of forest floor organic matter.

Early studies on the hydrologic role of the forest floor in the northeastern United States showed a decline in floor thickness after clear-cutting, and then a gradual recovery (Morey 1942; Sartz and Hutter 1950). The high leaching loss of nitrate from a devegetated northern hardwood forest in New Hampshire was attributed to rapid decomposition of the forest floor and conversion of its nitrogen to soluble nitrate (Bormann

and Likens 1979). These results led Covington (1981) to try quantifying changes in the total organic content and nitrogen content of the forest floor with time since clear-cutting. By sampling in 14 New Hampshire stands, Covington found a fairly steady decline in organic content to about age 15, and then a more gradual increase to precutting values by about age 70. He estimated that about 800 kg_N \cdot ha⁻¹ (kg_N, kilograms nitrogen) disappeared from the floor in the first 15 years after cutting, about half of the original amount. Little other data are available on the changes in forest floor organic matter or nutrient content over time through a clear-cutting rotation, although many studies have been done on secondary succession from old fields (e.g., Switzer et al. 1979).

Covington's (1981) results have played an important role in both qualitative discussion of the principles of ecosystem degradation and recovery (Bormann and Likens 1979) and quantitative simulation of nitrogen availability and tree growth during secondary succession in northern hardwoods (Aber et al. 1978, 1979, 1982). The simulation implied a severe reduction in productivity with rotation periods of 30 years and harvest of all aboveground material. Furthermore, Covington's mathematical formulation of his results has been used to study

¹Revised manuscript received June 13, 1984.

effects of forest management on the global carbon budget (Cooper 1983). However, in commenting on the shape of Covington's curve, Aber and Melillo (1982) state: "the degree and timing of decline and recovery in forest floor biomass is crucial to projections of management effects."

Because of the importance of Covington's results and questions about the rate of decline of forest floor, I decided to obtain additional data from the same vegetation type and geographic area, northern hardwoods of central New Hampshire. The objectives were to either verify or disprove the shape of Covington's response curve, to test a correction that he made for sampling bias, and to look for differences in forest-floor thickness, bulk density, organic fraction, and nitrogen fraction with stand age.

Methods

Ideally, a study of forest-floor dynamics would follow a site through time. However decades would be needed to cover a rotation. An alternative is to compare stands of different ages at the same time, while insuring as much as possible that the stands are all following the same sequence. Covington (1981) used many rejection criteria for stand selection (elevation, slope, aspect, species composition, etc.) and for selection of sample points within a stand. In this study, many of these restrictions were relaxed, partly to better generalize the results, and partly because even-aged stands from 10 to 50 years old are very rare in the area. Such stands have been located only after exhaustive search by many scientists and most have been used for many ecological studies.

The stand selection criteria which I used were fairly simple. The stands had to be northern hardwoods, dominated either by yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), or pin cherry (*Prunus pensylvanica* L.f.) in young stands. Conifers, poorly drained soil, extreme rockiness, steep slopes, mull humus, or older residual trees sufficed to exclude stands. Measurements were determined in 13 stands, 6 of which were in the Bartlett Experimental Forest.

Bartlett Forest stands

The forest floors of six stands in the Bartlett Experimental Forest of central New Hampshire were measured in the summer of 1979. The thickness of forest-floor horizons in each of these stands had also been measured in 1951 and 1959. Stand descriptions and thickness changes are given in Federer (1982). In 1979, six parallel lines of 10 points each, with 10 m between both points and lines, were established in each stand. A 10 × 10 cm block of the forest floor was removed at each point and separated into Oi, Oe, Oa, and A² horizons, and the thickness of each horizon was measured. For each of the six lines, the samples from the 10 points were composited by horizon. Samples were air dried and sieved to 2 mm with moderate rubbing; material less than 2 mm was weighed. Air-dry water content was determined by oven-drying a subsample at 80°C. This subsample was then ashed at 550°C for 3 h in a muffle furnace to measure organic fraction. Total nitrogen content for each horizon and stand was measured by block digest and Autoanalyzer³ on three samples composited from pairs of adjacent lines.

The Oi, Oe, and Oa horizons were defined as follows: the Oi horizon is unaltered dead remains, Oe is mostly fragmented, partly decomposed organic materials sufficiently well preserved to identify their origin, and Oa is mostly well-decomposed, amorphous organic matter. The A horizon was defined as a mix of organic and mineral soil

²Horizons are designated by the new United States Department of Agriculture Soil Conservation Service names.

³Trade or proprietary names are included for information purposes only and do not imply any endorsement by the Canadian Journal of Forest Research and the Forest Service of the United States Department of Agriculture.

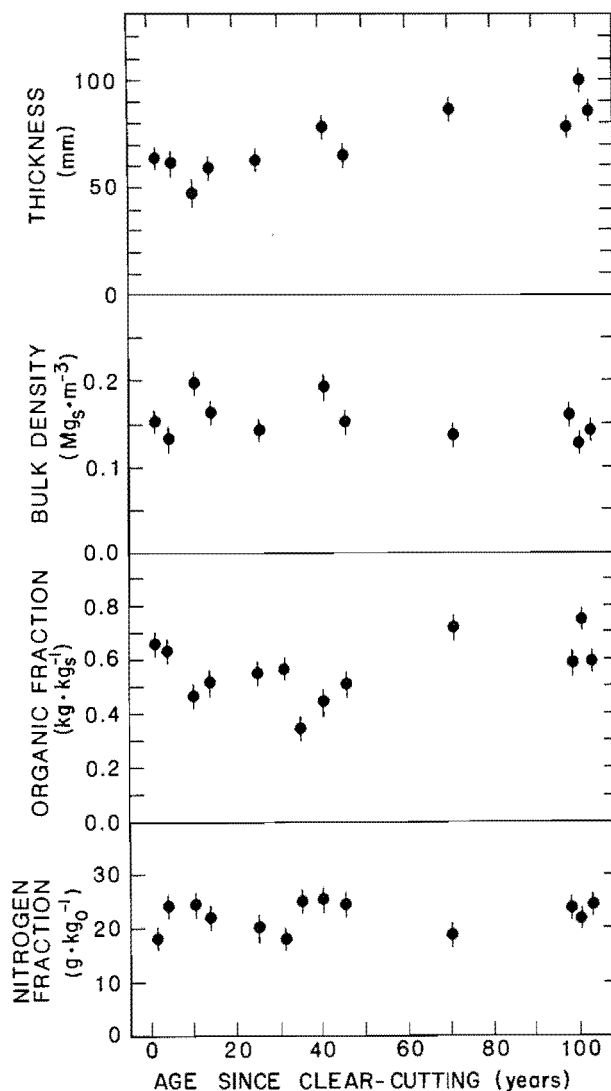


FIG. 1. Forest-floor thickness, bulk density, organic fraction of dry mass, and nitrogen fraction of organic matter versus stand age. Error bars are the standard error; $n = 5$ or 6 except for thickness, for which $n = 50$ or 60.

containing between 0.20 and 0.40 $\text{kg}_o \cdot \text{kg}_s^{-1}$ (kg_o , kilograms organic matter; kg_s , kilograms oven-dry soil); it is usually overlaid by an E eluviated horizon.

Other stands

In the summer of 1980, I measured seven additional stands. In these, the forest floor was not divided into horizons. Five, rather than six, parallel lines of 10 points each were laid out, with 10 m between both points and lines. A 10 × 10 cm block of forest floor was removed at each point and composited with the other points along a line to make one sample for each line. The five samples from each stand were air dried, weighed, and sieved to 1 cm. Air-dry water content was determined on one subsample. Two subsamples from each sieved sample were ground and combined before one measurement of organic matter and total nitrogen. Methods of analysis were the same as for the Bartlett stands. Thickness and, thus, bulk density were not obtained in two of the stands. Where A horizon material was found, it was included as part of the forest floor.

Results

Age differences

Total thickness of the forest floor was close to 60 mm in the

TABLE 1. ANOVA for forest-floor thickness. The linear and quadratic sums of squares do not add to the regression sum of squares because the two terms are not independent of each other

Source	Degrees of freedom	Mean square	F value
Regression	2	50.52	10.96
Linear	1	8.29	1.80
Quadratic	1	0.47	0.10
Between stands	8	4.61	1.95
Between lines	50	2.37	

five stands that were 1 to 24 years old; it was about 70 mm at age 40, and 80–100 mm in stands at least 70 years old (Fig. 1). Analysis of variance, including linear and quadratic regression terms for age, showed that the age effect on thickness was statistically significant (Table 1).

Bulk density, organic fraction, and nitrogen fraction of organic matter in the forest floor did not show any significant age effect by analysis of variance, including linear and quadratic regression terms for age. Bulk density of the forest floor ranged from 0.12 to 0.20 $\text{Mg}_s \cdot \text{m}^{-3}$ among stands; organic fraction ranged from 0.35 to 0.75 $\text{kg} \cdot \text{kg}_s^{-1}$; nitrogen fraction ranged from 17 to 25 $\text{g} \cdot \text{kg}_o^{-1}$ (Fig. 1).

The organic matter content of the forest floor on a unit-area basis is the product of the floor thickness, its bulk density, and its organic fraction. The total organic matter content of the forest floor in this study was about 80 $\text{Mg} \cdot \text{ha}^{-1}$ in old stands, but about 50 $\text{Mg} \cdot \text{ha}^{-1}$ at ages 4 through 24 (Fig. 2). Analysis of variance showed a significant age effect.

The nitrogen content of the forest floor on a unit-area basis was about 1.1 $\text{Mg} \cdot \text{ha}^{-1}$ in the younger stands and 1.6–2.0 $\text{Mg} \cdot \text{ha}^{-1}$ in the older stands. The age effect was significant.

Horizon differences

The thickness of each horizon in the Bartlett Forest floors was reported by Federer (1982). By comparing thickness of the floor in the 10-year-old stand with its measured thickness in 1959 before cutting, Federer (1982) showed evidence that Oi and Oe, and possibly Oa, horizons decreased in thickness after cutting.

Bulk density of the forest floor differed considerably by horizon. In the six Bartlett stands, Oi-horizon bulk density was between 0.02 and 0.04 $\text{Mg}_s \cdot \text{m}^{-3}$ in all samples. Bulk density of Oe generally was 0.08–0.15 $\text{Mg}_s \cdot \text{m}^{-3}$, while Oa was 0.14–0.24 $\text{Mg}_s \cdot \text{m}^{-3}$ and A was 0.20–0.60 $\text{Mg}_s \cdot \text{m}^{-3}$.

Organic fraction of the forest-floor horizons in the Bartlett samples was given by Federer (1982). Organic fraction of Oi material generally was greater than 0.8 $\text{kg} \cdot \text{kg}_s^{-1}$, whereas Oe samples contained between 0.5 and 0.9 $\text{kg}_o \cdot \text{kg}_s^{-1}$. Nearly all Oa samples had between 0.5 and 0.8 $\text{kg}_o \cdot \text{kg}_s^{-1}$, while A samples had between 0.15 and 0.50 $\text{kg}_o \cdot \text{kg}_s^{-1}$.

The nitrogen content as a fraction of organic matter is lower in Oi than in the other three horizons. The Oi-horizon means at Bartlett contained between 15 and 19 $\text{g}_N \cdot \text{kg}_o^{-1}$ with no age trend. In the Oe, Oa, and A horizons, nitrogen was 20–25 $\text{g} \cdot \text{kg}_o^{-1}$ with no apparent variation by horizon or stand age.

Discussion

Forest floor definition

The definition of the forest floor may vary among investigators (Federer 1982). In most forest-floor samples from White

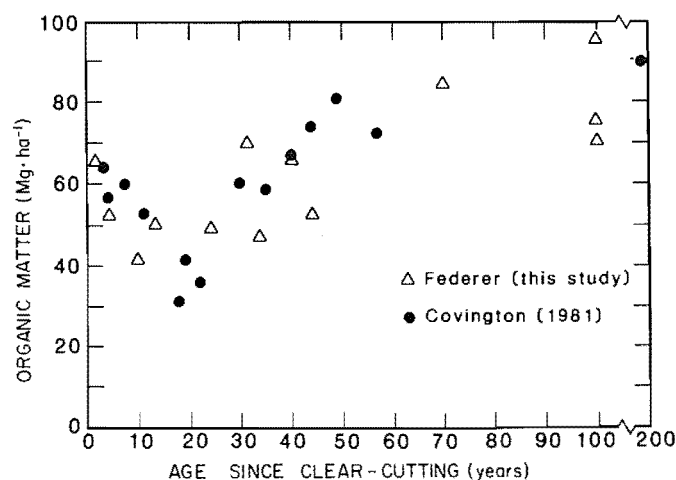


FIG. 2. Organic matter content of the forest floor in this study (Δ) compared with Covington (1981) (\bullet) without applying his adjustment.

Mountain northern hardwood stands, the break between Oa and E horizons is very sharp. But Covington (1981) stated: "In some cases the lowermost H-layer was mixed with very fine mineral soil which was then included in the forest floor sample." He did not further define the bottom of the forest floor. In this study, mixed organic and mineral material with organic content estimated by eye to be greater than 0.20 $\text{kg}_o \cdot \text{kg}_s^{-1}$ was called A horizon and was included in the forest floor. However that separation is now obsolete; the division between forest floor and mineral soil should be made at 0.40 $\text{kg}_o \cdot \text{kg}_s^{-1}$ (Federer 1982). Therefore, the forest floors in this study include some A material that should have been excluded. In the Bartlett samples, the organic fraction in the A horizons varied from 0.15 to 0.50 $\text{kg} \cdot \text{ha}^{-1}$ (Federer 1982). The organic content of the A horizons ranged between 6.3 and 22.8 $\text{Mg} \cdot \text{ha}^{-1}$ or between 7 and 35% of the total organic matter content of the forest floor. It is difficult to estimate how much of this material would have been excluded from the forest floor if the 0.40 $\text{kg}_o \cdot \text{kg}_s^{-1}$ organic matter criterion had been used. The difference is ignored hereafter, but it is clear that variation in definition could cause 10 or 20% differences in floor organic content.

Another problem of definition occurs in the sieve size used to define exclusions of stones, undecomposed wood, and roots. In this study, 2 mm was used for some stands and 1 cm for others. The difference is not evident in the data, and probably is less than 10% of the organic matter content. The standard 2-mm sieve is too fine for work with forest floor, but 1 cm is too large. It seems that 6 mm (0.25-in. hardware cloth) is an appropriate screen size to separate exclusions from the forest floor. The amount of rubbing and pressure used in sieving also varies and is difficult to standardize.

Organic content

My data for the total organic matter content in the forest floor agree remarkably well with Covington's (1981) data (Fig. 2) in spite of possible differences in stand selection, sample point location, and forest floor definition. In addition to the stand selection criteria mentioned in Methods and used by both of us, Covington selected stands within a fairly narrow range of elevation, slope, topography, and site quality. Within a stand, he placed additional restrictions on sampling points by avoiding disturbed areas, gaps in the canopy, rocks, large

roots, abnormal horizons, and windthrow mounds and depressions, whereas I sampled all of these except for major skidroads. Roughly, among 50 points in a stand, I found 3 with rotten wood, 2 with rocks at the surface, 2 with large roots, 1/2 at a tree base, and 1/2 with organic matter over rock. Covington would have excluded all of these points. Agreement of our results therefore indicates some compensating factors.

Covington (1981) recognized that his sampling restrictions might bias his results. By comparing his data for Watershed 6 on the Hubbard Brook Experimental Forest with that of Gosz et al. (1976), he suggested a multiplier of 0.65 to correct his figures for avoidance of areas of thin forest floor. However, agreement of my data with his implies that this multiplier is not justified. While his avoidance of windthrow mounds, rocks, roots, and tree bases would lead to overestimates, his avoidance of depressions and rotten logs or stumps evidently compensated.

Forest floor organic matter in so-called "mature" forests probably varies considerably with geography, soil drainage, and species composition. Mader et al. (1977) measured $63 \text{ Mg}_o \cdot \text{ha}^{-1}$ averaged over 28 New Hampshire hardwood stands, while stands in states farther south and west had lower amounts. Their data showed differences among drainage classes and between hardwoods and conifers. Hamburg (1984) measured $157 \text{ Mg}_o \cdot \text{ha}^{-1}$ in a White Mountain stand cut 120 years earlier, but this stand had a considerable number of conifers. Though the stands Covington and I measured were nearly free of conifers, the uncertainty about both past (prelogging) and future status of conifers in these stands makes the "climax" forest floor indeterminate. In the absence of conifers, the "shifting steady state" reached by northern hardwoods (Bormann and Likens 1979) appears to contain from 70 to $100 \text{ Mg}_o \cdot \text{ha}^{-1}$ in the forest floor (Fig. 2).

Partial or complete removal of the forest canopy causes increased decomposition rate in the forest floor (Piene 1978; Edwards and Ross-Todd 1983). The rate increase is usually attributed to increased soil temperature and moisture (Gorham et al. 1979). However, the greater magnitude of *fluctuations* of temperature and moisture after cutting may be more important than change in mean values (Lousier and Parkinson 1976; Piene 1978). A rapid reduction of forest floor organic content from approximately $80 \text{ Mg}_o \cdot \text{ha}^{-1}$ to approximately $50 \text{ Mg}_o \cdot \text{ha}^{-1}$ is produced in northern hardwoods within 10 years (Fig. 2). The change is caused by a reduction of floor thickness without significant change in bulk density or organic fraction.

In addition to increased decomposition, forest floor can also be reduced by mechanical mixing into the mineral soil during or after the harvest operation. The passing of machines and logs over the cut area churns, scrapes, and gouges the forest floor and the mineral soil. Complete mixing to 70 cm or more occurs in heavily used skidtrails, while other areas are less mixed. If the mixing leaves material that is less than $0.4 \text{ kg}_o \cdot \text{kg}_s^{-1}$ at the surface, then by definition, all of the forest floor has been eliminated by mixing or burying. In whole-tree harvested sites in New England, a majority of the area has had its forest floor affected by disturbance or mixing (C. W. Martin, personal communication). Salonijs (1983) describes several benefits of such mixing, including a reduction of the increase in decomposition rate. The relative contributions of decomposition and mixing in the sites we studied are not known. However, knowing which process dominates is critical because decomposition causes a permanent loss of organic matter, whereas mixing only redistributes organic matter within the system.

Covington's (1981) data show a rather steady decline in forest floor organic content to a sharp minimum about 20 years after cutting, and then a fairly rapid recovery. He fitted a mathematical relation to his data, but there seems to be no reason to use that specific relation. In their initial simulations of forest-floor dynamics in northern hardwoods, Aber et al. (1978) forced the model to fit the shape of Covington's mathematical curve. However, the more recent model of Aber et al. (1982) improves the feedback between regrowth and decomposition rate. This new model predicts a very broad flat minimum in forest-floor organic content from about year 5 to 25. The leaf area index, leaf litter, and presumably fine root litter in the regrowing forest recover to pretreatment levels in less than 10 years (Covington and Aber 1980). Microclimate changes causing increased decomposition should have disappeared by then. Aber et al. (1982) state that "it is difficult to explain how the forest floor could continue to decline for 20 years." Data from my stands could be interpreted as showing no change in organic content from age 5 to 25, which agrees well with the more recent simulation.

However, there is disagreement between the model of Aber et al. (1982) and the measured data in two other respects. First, the model gives the organic content of a "mature" forest floor as being about $53 \text{ Mg}_o \cdot \text{ha}^{-1}$, in agreement with Covington's (1981) corrected value. As I have already pointed out, the correction is not justified; measured values of approximately $80 \text{ Mg}_o \cdot \text{ha}^{-1}$ are more likely for forests over 60 years in age. Second, the model produces much slower recovery than the field data indicate. The model includes rather complex handling of litter of different sizes. The difference may lie in the decomposition rates used in the model for larger sizes of litter, or in the inclusion of some rotten wood in the field measurement of forest floor that is still separated out as "litter" in the model.

There is a speculative mechanism for continued decline to age 20. Although not statistically significant, my data suggest that the organic fraction of the forest floor may decline slowly to a minimum around 40 years after cutting (Fig. 1). The cutting disturbance could have a long-term effect on organism populations and on organic matter biochemistry. Visual observation suggests that a less distinct break occurs between forest floor and mineral soil in stands aged 10 to 45 years. On the Bartlett sites, the three younger stands had thinner H and thicker A horizons than the three old stands (Federer 1982). These observations are consistent with movement of organic matter downward into mineral soil, thus lowering the level of the bottom of the forest floor. The forest floor thickness could thus be increasing while its organic content was decreasing.

If the minimum is really flat and prolonged, then Covington's two lowest data points must be viewed as statistical extremes. Unfortunately my additional points have not answered the question. At present, it also seems doubtful that additional even-aged stands in the 10- to 30-year-age class can be found. Description and simulation of ecosystem response to clear-cutting should consider the possibilities of either a rapid decline to a broad flat minimum or a gradual decline to a sharp minimum. The two different interpretations, however, imply quite different dynamics of nutrient availability, particularly for nitrogen.

Nitrogen

Nitrogen content is closely tied to organic matter content. Both Covington (1981) and I found the nitrogen content of the

organic matter in the forest floor to be independent of stand age. His overall mean value was $25 \text{ g}_\text{N} \cdot \text{kg}_\text{O}^{-1}$ while mine was $22 \text{ g}_\text{N} \cdot \text{kg}_\text{O}^{-1}$. Hamburg (1984) recently reported a mean of $22.6 \text{ g}_\text{N} \cdot \text{kg}_\text{O}^{-1}$ for forests on abandoned agricultural land in the same geographic area. Using a value of $24 \text{ g}_\text{N} \cdot \text{kg}_\text{O}^{-1}$ gives about $1.9 \text{ Mg}_\text{N} \cdot \text{ha}^{-1}$ for mature stands and about $1.1 \text{ Mg}_\text{N} \cdot \text{ha}^{-1}$ for the minimum on the age curve. The forest floor in northern hardwoods loses $800 \text{ kg}_\text{N} \cdot \text{ha}^{-1}$ within 20 years after clear-cutting, but it is difficult to explain where all of this nitrogen goes.

Leaching, uptake by regrowth, sequestering in slash and fine roots, and denitrification are all possible nitrogen sinks (Aber et al., 1983). In northern hardwoods, as much as $200 \text{ kg}_\text{N} \cdot \text{ha}^{-1}$ can be lost by nitrification and subsequent leaching (Hornbeck 1977). Covington (1981) estimated that about $160 \text{ kg}_\text{N} \cdot \text{ha}^{-1}$ was taken up by regrowing vegetation in the first 15 years. Leaching and regrowth are quantifiable sinks but still leave roughly half of the missing nitrogen unaccounted for (Bormann and Likens 1979).

Covington (1981) suggested incorporation into decomposing slash through translocation by fungi. D. L. Mader (personal communication) believes that initial decomposition of large roots after cutting could be another temporary nitrogen sink. Later decomposition of both slash and roots would then contribute to the later recovery of organic matter and nitrogen by the forest floor. Fine root death may be a temporary sink (Aber et al. 1983) but cannot create long-term removal; much of the nitrogen in fine roots is included in the forest floor by the sieving technique used here.

Bormann and Likens (1979) mentioned both denitrification and mixing into mineral soil as possible sinks. Because nitrification follows cutting in these stands (Bormann and Likens 1979), and the soil is wetter, denitrification may occur. Among some of the same stands used in this study, Melillo et al. (1983) obtained a maximum possible rate of denitrification of $52 \text{ kg}_\text{N} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ in a 2-year stand. The real value must be much less than this, but the possibility is established that denitrification can account for some of the missing nitrogen. A final possibility is the movement of organic matter and the nitrogen it contains into the mineral soil by mixing during the harvest operation and by the speculative later movement of organic matter. Measurements of denitrification and organic matter movement are needed to close the forest floor nitrogen budget.

Quantification of the fate of nearly half of the forest floor organic matter and its nitrogen is very important for research on long-term productivity. If the organic matter and nitrogen are totally lost from the forest ecosystem, productivity loss from short rotation harvesting may be severe. If the organic matter and nitrogen are only moved within the system, short rotations may be practicable. The real situation probably lies between the two extremes.

Acknowledgments

I thank Ed Russell, Holly Zirkle, Jane Hislop, and Tim McDevitt for their assistance in field and laboratory work. Some sites were found with the help of the staff of the White Mountain National Forest.

ABER, J. D., D. B. BOTKIN, and J. M. MELILLO. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res.* **8**: 306–315.

———. 1979. Predicting the effects of different harvesting regimes on

productivity and yield in northern hardwoods. *Can. J. For. Res.* **9**: 10–14.

ABER, J. D., and J. M. MELILLO. 1982. FORTNITE: a computer model of organic matter and nitrogen dynamics in forested ecosystems. *Univ. Wis. Coll. Agric. Life Sci., Res. Div. Bull. No. R3130*.

ABER, J. D., J. M. MELILLO, and C. A. FEDERER. 1982. Predicting the effects of rotation length, type of harvest and fertilization on sustainable yield in northern hardwood forests. *For. Sci.* **28**: 31–45.

ABER, J. D., J. M. MELILLO, C. A. MCCLAUGHERTY, and K. N. ESHLEMAN. 1983. Potential sinks for mineralized nitrogen following disturbance in forest ecosystems. *Ecol. Bull.* **35**: 179–192.

ANONYMOUS. 1973. Forest fertilization symposium proceedings. USDA For. Serv. Gen. Tech. Rep. NE-3.

BORMANN, F. H., and G. E. LIKENS. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

COOPER, C. F. 1983. Carbon storage in managed forests. *Can. J. For. Res.* **13**: 155–166.

COVINGTON, W. W. 1981. Changes in forest floor organic matter and nutrient content following clearcutting in northern hardwoods. *Ecology*, **62**: 41–48.

COVINGTON, W. W., and J. D. ABER. 1980. Leaf production during secondary succession in northern hardwoods. *Ecology*, **61**: 200–204.

EDWARDS, N. T., and B. M. ROSS-TODD. 1983. Soil carbon dynamics in a mixed deciduous forest following clearcutting with and without residue removal. *Soil Sci. Soc. Am. J.* **47**: 1014–1021.

FEDERER, C. A. 1982. Subjectivity in the separation of organic horizons of the forest floor. *Soil Sci. Soc. Am. J.* **46**: 1090–1093.

GORHAM, E., P. M. VITOUSEK, and W. A. REINERS. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annu. Rev. Ecol. Syst.* **10**: 53–84.

GOSZ, J. R., G. E. LIKENS, and F. H. BORMANN. 1976. Organic matter and nutrient dynamics of the forest floor in the Hubbard Brook Forest. *Oecologia*, **22**: 305–320.

HAMBURG, S. P. 1984. Effects of subsistence agriculture and subsequent regrowth on soil nitrogen and organic matter pools. *Proc. 6th North Am. For. Soils Conf.* In press.

HORNBECK, J. W. 1977. Nutrients: a major consideration in intensive forest management. USDA For. Serv. Gen. Tech. Rep. NE-29. pp. 241–250.

KIMMINS, J. P. 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. *For. Ecol. Manage.* **1**: 169–183.

LOUSIER, J. D., and D. PARKINSON. 1976. Litter decomposition in a cool temperate deciduous forest. *Can. J. Bot.* **54**: 419–436.

MADER, D. L., H. W. LULL, and E. I. SWENSON. 1977. Humus accumulation in hardwood stands in the northeast. *Mass. Agric. Exp. Stn. Res. Bull. No. 648*.

MELILLO, J. M., J. D. ABER, P. A. STEUDLER, and J. P. SCHIMEL. 1983. Denitrification potentials in a successional sequence of northern hardwood forest stands. *Ecol. Bull.* **35**: 217–228.

MOREY, H. F. 1942. The application of our knowledge of the organic layers of the soil profiles to flood control. *Proc. Hydrol. Conf., Pa State Coll. Sch. Eng. Tech. Bull. No. 27*. pp. 143–151.

PIENE, H. 1978. Effects of increased spacing on carbon mineralization rates and temperatures in a stand of young balsam fir. *Can. J. For. Res.* **8**: 398–406.

SALONIUS, P. O. 1983. Effects of organic–mineral soil mixtures and increasing temperature on the respiration of coniferous raw humus material. *Can. J. For. Res.* **13**: 102–107.

SARTZ, R. S., and W. D. HUTTINGER. 1950. Some factors affecting humus development in the northeast. *J. For.* **48**: 341–344.

SWITZER, G. L., M. G. SHELTON, and L. E. NELSON. 1979. Successional development of the forest floor and soil surface on upland sites of the east Gulf coastal plain. *Ecology*, **60**: 1162–1171.